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# A SKETCH OF THE HISTORY OF REFLEX ACTION IN THE LATTER HALF OF THE NINETEENTH CENTURY.<sup>1</sup>

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## I

### A STATEMENT OF THE THEORY AND OF THE EXTENT OF KNOWLEDGE WITH REGARD TO REFLEXES AT THE TIME OF THE LOTZE-PFLÜGER DISCUSSION (1853.)

Before making in greater detail the statement which is the subject of this section it seems well, in order to bring the reader into touch with the development of knowledge of reflexes previous to 1853, to give in brief form a running account of the comprehensive article by Doctors G. S. Hall and C. F. Hodge in the *American Journal of Psychology*, Vol. III. These papers present a sketch of the history of Reflex Action from the earliest studies thereof to the time when Lotze made his famous reply to Pflüger and formulated the theory of reflexes which bears his name.

It is there shown how, at first, the soul was supposed to be able, without the mediation of any bodily mechanism whatever, to create sympathy between different parts of the body. The type of mind of the early physiologists was theoretical rather than scientific. Indeed, so long as those early investigators were explaining bodily functions of every character by reference to an immaterial soul inhabiting the natural channels of the body, and acting directly upon matter according to its

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<sup>1</sup> The writer wishes to express his obligation to Dr. E. C. Sanford, on whose suggestion this work was undertaken and by whose counsel it was carried to completion.

own freedom, no scientific physiology was possible. But as time advanced new phenomena were discovered which could not be classified under existing theories, and the new hypotheses to which they gave rise only increased the confusion.

Harvey discovered in 1628 that the arteries and veins during life are filled with flowing blood. The supposition that these channels, empty after death, were during life the avenues for animal spirits had to be abandoned; and Robert Whytt advanced the matter to a new stage by his explanation of the phenomena of life by the "power or influence of the nerves." The current was setting toward the Newtonian ideal, the maintenance of steadfast communication with facts.

Very early it had been found that some nerves when stimulated mediate sensation, others motion. It was left, however, for Charles Bell to show, and for Magendie more conclusively to demonstrate, that the posterior spinal roots are sensory, and the anterior motor. The way was then opened for further classification of phenomena. The anatomical elements concerned in reflex action, viz.: a centripetal and a centrifugal nerve with their part of the spinal cord, were known, and the next question was, "do these parts operate on mechanical principles or not?"

The first reply to this great question was in the affirmative. Marshall Hall (1837) first proposed a mechanical theory of reflex action. He assumed a special excito-motor system in the cord and said: "There is nothing whatever that can be called psychic about any of its activities." He was enthusiastically supported by his German translator, Kürschner, who said that the activity of ganglia incites motion "as water drives a mill." Volkmann (1838), on the other hand, declares that in the lower animals, at least, it is certain that the sensitive principle is divisible; that, therefore, whenever the central nervous system be divided a portion of this principle remains on both sides of the section. Such animals cannot then be pure mechanisms as Marshall Hall had supposed. Volkmann, however, is not sure that this principle is valid for the higher animals.

Pflüger was bolder. Following in the footsteps of Volkmann, he violently asserts that consciousness (which he regarded as a form of motion) is, whether we call it "Sensorium" or "Soul," capable of division with the body. The spinal cord, then, has its soul; every portion of the body which, independently, is capable of responding to a stimulus, possesses a soul. "Reflex action is the operation of a neuro-physic mechanism by means of which the sensory fibre through the cord, changes the ordinary state of excitation of definite motor nerves."

This brings us to Hermann Lotze and to the beginning of that period which furnishes the material for the following sections. In the Lotzean theory the soul has nothing to do directly in the production of reflex actions. Under certain limitations the theory may be described as mechanical; but all movement, whether of the intact animal or the reflex preparation, is proximately or remotely subject to the psychical. The starting point of all movement is in the soul. "If we call to mind, consequently, that activities earlier performed in consciousness have left behind not only unconscious memories in the soul, but also physical impressions in the central parts of the nervous system, we can consider purposive and adaptive movements to be dependent upon these impressions as well as upon a soul still in existence. For even the soul itself in the production of these movements should be considered not as an intelligent substance but as a substance with enduring states standing in reciprocal relation with one another and reproducing one another."

"The origin of certain movements of beheaded animals we seek not in an intelligence yet living, but in one which exists only in its after-effects. We believe that an animal body whose soul has had no experiences, or which has not worked out some experience into a life of ideas, would not be in a condition to perform those movements after the excision of its brain; we consider it not as a mechanism of the first construction, but as one of practice. When, under the influence of the soul life an association has once been formed between the mere physical impression of a stimulus and a movement which is not united with that stimulus by the mere relation of structure and function, and when that association has been firmly established, this mechanism can continue the activity without requiring the actual assistance of intelligence."

"In animal bodies examples of such habituation in function to which the influence of mental life does not extend are by no means wanting. Yet, much more frequently, we find them in the sphere of movements. Not only are almost all reflex movements produced the more easily and by slighter stimuli the more frequently they occur, but even the voluntary movements through practice become graceful and manageable. Many gestures, originally arising by chance, have gradually become customary, and we find them firmly and ineradicably rooted; finally the acquired mien, movement, and grace of the body is frequently transferred from generation to generation, which could hardly occur if the repeated function were not fixed in a remaining disposition of the central organs, and hence, were not capable of transplantation. As stature has placed at the disposal of the soul a principality of automatic

implements, the activity of the mind reacts upon it, giving it dignity, and the body is impregnated by the attainment of an intelligence which, nevertheless, is not identical with it, is not diffused through it, and at the same time is not separable from it."<sup>1</sup>

According to this theory the movements of the eel's tail away from the flame, and the purposive movements of the decapitated frog, cited by Pflüger as indications of a spinal soul, are not due to the presence of a soul in the cord, but to the after-effects of conscious activity impressed upon a plastic organization and transmitted by heredity. Lotze had, therefore, caught the idea of development from the conscious to the unconscious; the voluntary to the involuntary; from the spontaneous to the reflex; and we shall hope to see in the succeeding sections how this theory has stood the test of fifty years.

We shall now turn to a brief examination of the state of experimental knowledge of the physiology of reflex action at the time in question.

Among the most numerous observations are those by Pflüger, and since they suggested so many lines of research for the investigators who were to follow, his experiments are of great importance. He believed that reflex actions are best studied in men, especially in human pathological cases, and on the results of such studies he based his five laws of reflex action: the law of Unilateral Reflexes; of Reflex Symmetry; of Unequal Contraction on the Two Sides; of Reflex Irradiation; of the three Locations of Reflex Contraction. These laws were illustrated by many experiments on frogs, eels, and salamanders, and from these he concludes that sensory and motor nerves end in their respective levels of the cord, not in the brain which many regarded as the only organ of sensation and volition. As might be expected from a study of the Lotzean theory, its author declares that Pflüger's crucial experiments are too uncertain to warrant the inferences drawn from them.

It seems measurably correct to visualize the course of the studies of reflex action preceding the Lotze-Pflüger discussion as lying along the main trunk line of "physical" reflexes as they were then called; *i. e.*, bodily movements of defense against attacking stimuli. Nevertheless there had been some minor observations of the movements of the internal organs which were called "organic" reflexes, and which opened the way for later thorough investigations made possible by the discovery of improved devices for experimental observation, and improved methods of operation.

What has now become an almost impenetrable jungle of

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<sup>1</sup> Lotze: *Gelehrte Anzeiger*, Göttingen, 1853, III, pp. 1737 ff.

literature on the inhibition of reflex action sprang from seeds sown by Marshall Hall, though the phenomenon was not subjected to detailed examination until a quarter of a century had passed. The observation made by Hall is now a commonplace with every amateur experimenter with reflex actions, viz.: that reflex movements cannot be produced in the first moment after decapitation. Whether this is due only to the shock to the central nervous system, as is now very generally believed, or to stimuli from the cut surfaces, is left for future determination. A typical instance of the restraining influence of nervous centres upon a particular bodily organ is the inhibitory effect of the vagus upon the heart. This was discovered by the Webers in 1844,<sup>1</sup> and almost forty years later McKendrick called it the "most recent advance in *nervous physiology*."<sup>2</sup> Our present knowledge of inhibitory phenomena, in detail, was, however, in 1853, scarcely begun.

Physiologists were not introduced to the summation of stimuli until the year following the discussion between Lotze and Pflüger, when Eduard Weber computed the rate of transmission in sensory nerves; and no really systematic work was done on the subject until nearly a score of years later.

Neither had the knowledge of vascular tonus made much further progress than that of inhibition, though Legallois, as early as 1830 or before, had observed that the circulation of the blood ceases much more quickly than otherwise if the spinal cord be destroyed after decapitation. And changes in the lumen of blood vessels had been observed from time to time. Indeed, it may be doubted whether, within the period of which we are now writing, at any rate until its very close, the tonicity of the vascular system was ever regarded as reflex. We have such eminent authority as J. Lister and Gruenhagen to support the statement that a notion of the reflex nature of the tonus of the vascular system begins with Claude Bernard in 1852 and Augustus Waller in 1853. For Bernard in the year named had shown that if the sympathetic nerve in the neck of a cat be severed the blood vessels on the wounded side become turgid, and the temperature of the parts is heightened. Waller, in the year following, completed the demonstration by showing that if the nerve above the point of section be stimulated by an electric shock, turgescence ceases and temperature subsides.

This bit of experimental knowledge forms an indispensable nucleus about which later scientists have built a vastly complicated structure. The cause of a reflex muscular tonus, on the other hand, is within this period much less clearly conceived.

<sup>1</sup> Artikel—Muskelbewegungen—Wagner's Handwörterbuch d. Phys. Bd., III, Abth 2 p. 47, 1844.

<sup>2</sup> McKendrick: A Lecture on Physiological Discovery. *Brit. Med. Jour.*, 1883, I, p. 708.

The term "tonus" was first used by J. Müller<sup>1</sup> to describe the tense condition of muscles in a state of rest, and Henle assumed that it is to this slight tension of the muscles of the face that we owe our natural facial expression. This tension was supposed to be dependent upon the constant influence of the central nervous system, and Hall and Volkmann shared the view. Although Ed. Weber, in 1844, revolted against the theory of such a muscular tonicity, it was the prevailing view held at the end of the period covered by the present chapter, and the strong reaction against it led by Auerbach and Heidenhain, distinctly marks the beginning of the following period of the study of muscular phenomena.

The tendon reflexes did not attract the attention of physiologists until nearly a quarter of a century after the beginning of the period we are reviewing.

If we except, then, the discovery of the inhibitory effect of the vagus upon the heart by the Webers, we see that the chief results obtained previous to 1853 were in the field of the bodily or limb reflexes which led to the formulation of Pflüger's laws. Thereafter, as a result of more delicate means of observation, increasing attention was given to the uniform and varied movements of the vital organs. The notion of the reflex character of organic behavior steadily encroached upon the field of the unknown. The reflex arc took the place of many a supposed spontaneous activity, and investigators since that time have gradually left the highways of philosophy for the intricate byways of physiological experiment. They have become more interested in the collection of facts than in their correlation; and more and more dominated by a desire for "pure" science. This is very likely the spirit in which all great achievements have been won, but it is likewise the spirit which leads to the production of a mountain of details, inexhaustibly rich in definite suggestions to other investigators and bewildering to those who attempt to set them in order.

So few within this period are the generalizations and discoveries of general importance to the comprehension of reflex action that it is difficult to make clear cross sections of the whole and to treat all between in a single chapter. We may, with considerable justification, consider the beginning of our fifty years as the point in the main current of our knowledge of reflexes where the stream breaks up into many parallel branches.

We shall, therefore, for the sake of convenience, treat these separately in their physiological groupings.

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<sup>1</sup> J. Müller: *Handbuch d. Physiol.*, 1837, Bd. II, p. 29.

## II.

## THE INHIBITION OF REFLEXES.

The problem of reflex inhibition is everywhere veiled in uncertainty. Consensus of opinion on this subject seems like a "Will o' the Wisp;" now almost at hand, the next moment far out of reach. And to-day our knowledge of the matter is hardly in a more settled state than it was a score and more of years ago.

This uncertainty is due, doubtless, to the difficulties that lie in the way of experimentation. Goltz, for instance, has shown<sup>1</sup> that after an operation has been performed, and the wound has healed, we have to deal with the vicarious functions of other parts. Hence we can never tell just what are the inhibitory functions of the injured part. Luciani has also called attention to the fact that we can never be sure how soon after the operation degenerations have begun in the cord nor how rapidly they have extended,

Following the discovery by the Webers of the influence of the vagus upon the heart, physiologists turned their attention especially to the function of this nerve. Schiff and Moleschott erroneously concluded from numerous experiments that it is motor to the heart. Pflüger, however, in his characteristically vigorous, not to say pugnacious, way demonstrated beyond a doubt that the heart is inhibited by the vagus nerve.<sup>2</sup> If the simplest rules of experimental practice in the application of electrical stimuli be employed, *i. e.*, if the vagus be isolated, no motor effect is discernible. On the contrary, as he says by way of conclusion: "The stimulation that retards the frequency of the pulse manifests itself on the heart through no other symptom than the prolongation of the diastole. If the vagus, as Schiff and Moleschott assert, can increase the frequency of the pulse, even in the face of high exhaustibility, at least the diastole must be shortened and contraction prolonged. Instead of this only the first is seen: prolongation of diastole." Pflüger seems to have observed the phenomena very accurately, for Howell, in 1896, agrees with him in describing the effect of vagus stimulation. How the vagus inhibits, however, and how the heart is excited to activity, are matters less easily decided. Stewart found, in 1892, that during moments of greatest intra-cardiac pressure it is most difficult to inhibit the pulsation of the heart by stimulation of the vagus. This seems to indicate that the motor apparatus is located in the muscular walls of the organ itself. Of recent

<sup>1</sup>Goltz: Ueber d. Verrichtungen d. Grosshirns. *Pflüger's Arch.*, XIII, pp. 1 ff.

<sup>2</sup>Pflüger: Untersuch. aus d. Bonner physiolog. Lab., 1865, pp. 1 ff.



times the most widely accepted explanation of inhibition by the vagus is that which Stefani proposed in 1880, and Gaskell somewhat later. The vagus is the trophic nerve of the heart. It is katabolic in systole and anabolic in diastole. The after effect of vagus excitation, says Gaskell<sup>1</sup> somewhat later, is to strengthen the force of the cardiac contraction and to increase the speed with which excitation waves pass over the heart. The contrary effects on the other hand appear on stimulation of the augmentor. This theory of vagus inhibition as due to trophic effects is not without positive experimental evidence, for Fantino, in the same year in which Gaskell wrote his defense of the theory, cut the left vagus in a rabbit and reported the changes which he observed in the heart wall. The animal was apparently healthy, ate well, and its weight increased. But on examination eighteen days after the operation it was found that the heart had atrophied to a considerable extent. The region over which the waste of tissue occurs, moreover, differs according as the right or left vagus is injured.

There are but three theories which have at any time received wide acceptance.<sup>2</sup> None of these can be sharply limited chronologically or by generally important physiological discoveries. They are tenacious of life and each overlaps the period during which the succeeding theory attained its prime.

*Setschenow's Centre Theory.* The first is known as Setschenow's centre theory.<sup>3</sup> Setschenow discovered that while stimulating the optic lobes and mid-brain of a frog reflex movements of the limbs could not be induced by peripheral stimulation as under ordinary circumstances. These parts he calls the centre for inhibition. They are kept in tone by continuous sensory impressions. This theory has enjoyed a long life. Even to-day some eminent physiologists have not positively decided against it. Tigerstedt, for instance, in 1897, gives it as his opinion, that it must be considered as undecided whether inhibitions can be explained by the centre theory.<sup>4</sup>

Setschenow was at first inclined to the opinion that the

<sup>1</sup>Gaskell: *Arch. de Physiol.*, 1888, I, pp. 56 ff.

<sup>2</sup>Of the explanations offered for particular cases of inhibition we cannot now speak, but must pass on to trace the development of the theories of inhibition in general. One of the earliest theories was offered by Schiff who believed that inhibition was merely a case of exhaustion. Pflüger held a theory of special inhibitory ganglia in the heart and intestinal walls and elsewhere, a theory which was more satisfactory at the time. There were also other minor theories, but none have more than an antiquarian interest at the present time.

<sup>3</sup>Setschenow: *Phys. Studien über d. Hemmungs-Mech. f. d. Reflex-thätigkeit d. Rückenmarks d. Frosches*, 1863, pp. 1-71.

<sup>4</sup>Tigerstedt: *Physiol. d. Menschen*, Bd. II, 1897, p. 285.

inhibitory centres lie only in those parts of the brain which have been mentioned, because direct stimulation of the surface of a transverse section of the cord has not the same effect as stimulation of the optic thalami. This, however, was later shown to be insufficient, and when Herzen and Schiff showed that, in a completely debrained frog, stimulation of the posterior parts inhibits the movements of the fore limbs, Setschenow extended his theory and declared that inhibitory centres exist also in the spinal cord.

Preyer supported the theory of inhibitory centres on the ground of his observations of the phenomenon of kataplexy<sup>1</sup> and explained hypnosis by inhibition. Of the inability to produce violent movement during the kataplektic state, he says: "The excitation of the reflex inhibitory apparatus outweighs that of the psychomotor centres." Nothnagel in his argument for the centre theory even went so far as to ascribe to the inhibitory centres the power of voluntary activity.

It had been explained that there were definite inhibitory centres in the brain and spinal cord, and the followers of Setschenow attempted to discover the avenues through which excitations from the periphery reach these centres. Setschenow himself had considered the eye as the chief medium for this purpose, but Langendorff, on repeating Goltz's experiments on the reflex croak, and finding that by pinching the frog's toe the croak could be inhibited, concluded<sup>2</sup> that the skin was another avenue for these excitations. Inhibition was, he thought, purely reflex.

But, as Schlösser pointed out, if one grants all that the experiments seem to show there is no indication as to how these centres can act,<sup>3</sup> and further, in order to account for the numerous inhibitions actually found, the centres must be exceedingly numerous or must form a very complex system. Goltz comments upon this same difficulty as follows:<sup>4</sup> "Many have undertaken to assume (for the explanation of numerous experiments, which may be made clear much more simply in another way) inhibitory centres in the heart. These should be inhibitory centres of the first order. The heart is brought to a standstill by the mediation of the vagus nerve from the medulla oblongata; therefore in the medulla there would be an inhibitory centre for the heart which should be the inhibitory

<sup>1</sup> Preyer: Die Kataplexie u. d. thierische Hypnotismus, Sammlung, phys. Abhandlungen, Jena, 1875, Secs. 17-42.

<sup>2</sup> Langendorff: *Du Bois Reymond's Arch.*, 1877, 4 u. 5 Heft, pp. 96-115 and 435-442.

<sup>3</sup> Schlösser: Untersuch. über die Hemmung von Reflexen. *Du Bois Reymond's Arch.*, 1880, pp. 303-322.

<sup>4</sup> Goltz: Nervencentren d. Frosches, 1869, p. 50.

centre of the second order. This inhibitory centre can, however, as I have shown, be inhibited if the skin of the extremities is strongly stimulated. For this we need an inhibitory centre of the third order to bring the centre of the second order into a state of inactivity. . . ."

Moreover, there are anatomical difficulties in the way of the full acceptance of such a theory as Setschenow's. It is a plausible theory that if there are specific centres for all inhibition there must also be special inhibitory nerves for voluntary muscles as well as for the heart and intestines. The question has been amply discussed both pro and con. Wundt tells us<sup>1</sup> that there are inhibitory nerves leading to muscles and to glands. They are most probably connected with the muscles by reflex inhibitory ganglia. But Amaya points out<sup>2</sup> that while it may be assumed that inhibitory fibres are contained in the nerve trunks they cannot be isolated from the motor fibres by any process of degeneration. A still further difficulty with the centre theory, which Setschenow himself admitted, and which shows its incompleteness, is that by it the inhibition of the tactile reflexes cannot be explained since for these Setschenow failed to find any specific centres.

*The Theory of Goltz.* The unreasonableness of having to explain the inhibitions of different reflexes by different theories led Goltz to offer a new explanation. This was more theoretical than the former, but its author hoped it would cover all cases. He proceeds from the inhibition of the croak in the frog, which he calls a good type of all inhibitions. The hypothesis rests upon the supposition that "a centre which mediates a definite reflex act loses excitability for this act if it is set in excitation at the same time by any other nerve tracts which are not concerned in that reflex act." The inhibition of tactual or other reflexes, says Goltz, can be explained on this theory, and this constitutes its great advantage. If a reflex frog's flank be acidized, the spot is wiped by the foot of the adjacent side, whereas the normal frog leaps away. From the ever active brain, he says, excitations are always flowing to every centre; and thus, it comes about that in the normal frog the movement to wipe off the acid is suppressed, and the movement of escape is substituted for it.

Wundt also discusses the influence of the higher centres upon the occurrence of reflexes.<sup>3</sup> "This point of view," he says, "casts light upon the slighter intensity of reflexes which one generally observes so long as the brain is retained. In this

<sup>1</sup>Wundt: *Lehrb. d. Physiol.*, 1878, p. 528.

<sup>2</sup>Amaya: *Ueber scheinbare Hemmungen aus Nervmuskelpreparate*, I u. II, 9te u. 10te H., pp. 413 ff. 425 ff.

<sup>3</sup>Wundt: *Mechanik d. Nerven*, 2te abth., 1876, p. 100.

case simultaneously with the stimulation of the reflex organ occurs also a stimulation of the brain in which conscious sensation arises. The sensation is probably only an accompanying phenomenon and stands in no direct relation to inhibition. But according to the rule that every interfering stimulation of the central spheres in which centripetal fibres end inhibits reflexes, so in this case also, through the interference of spatially separated stimulus-effects of one and the same stimulation, an inhibition can occur."

This explanation, says Goltz, has in it many points of similarity with the theory previously offered by Herzen and Schiff, viz.: that inhibitions are due to the exhaustion of nerve centres. Herzen had said that any strong sensory excitation removes the reflex excitability of the nerve centres because they are exhausted by the intensity of the excitement. On the other hand Herzen's contention that reflexes are heightened by the debraining operation because thereafter the sensory excitations have a narrower sphere in which to be effective, is not approved by Goltz for a reason similar to that offered by Wundt, namely, that inhibitions are more intense the better the condition of the animal for the transmission of stimuli.<sup>1</sup> There are numerous phenomena to support this objection.

Taken as a whole the literature contains fewer direct references either of approval or condemnation of this view than that of Setschenow, but there are many who lend it their support by implication. Among these is Wundt, who thinks that when two or more excitations reach a sensory centre their effect is inhibition.<sup>2</sup> Howell, too,<sup>3</sup> says that to obtain inhibition, there must be at least two pathways by which impulses may reach a cell, and the stimuli conveyed over these different tracts must tend to excite different reactions. Inhibition, therefore, is connected with the effects of sets of impulses upon a responding cell, and this is associated with the fact that as the two paths end in different relations to the cell the impulses must enter it at different points, and hence, tend to act on different portions of the cell contents. There is enough known, he says, to conclude that inhibition does not depend upon special fibres but upon several impulses coming in by different paths. Schlösser, however, is one of those who opposes this theory.<sup>4</sup> He is convinced that all the phenomena of inhibition can be explained on the supposition of antagonistic centres, and is unable to find any proof for the disturbance of an excitation within the cell. In fact, such proof, it may be said in passing,

<sup>1</sup> Wundt: *Physiol. Psychol.*, 5 te Aufl., Bd. I, 1902, p. 86.

<sup>2</sup> *Op. cit.*, Bd. I, p. 87.

<sup>3</sup> Howell: *Am. Text Book of Phys.*, 1896, p. 667.

<sup>4</sup> Schlösser: *Op. cit.*, pp. 303-322.

cannot be experimental, and Goltz himself did not expect to find it. Tigerstedt leaves the question open. Verworn approaches the matter in an attempt to answer the question: "What relation exists between a centre and a muscle when a muscular contraction is inhibited?"<sup>1</sup> He was able to disprove the assertion of Starke that in inhibition of skeletal muscles the excitability of motor roots is reduced. On the other hand he says this excitability is unchanged. Hence there is no active inhibitory impulse opposed qualitatively to a motor impulse conducted to a muscle through its nerves. In other words: "The process of inhibition arising in the ganglion cell bodies of the anterior horns is not extended to the axis cylinder of the neurones, and is not transmitted through them to the skeletal muscles, nor transmitted actively in any way." He further concludes that skeletal muscles also possess no particular inhibitory fibres; that all inhibitions which occur in the skeletal muscles, *e. g.*, reflex inhibitions, are purely passive, and occur only in a central way through inhibitions of the central elements, and consequently consist only in a simple cessation or dropping out of the central excitatory impulses to the muscles. On the other hand he does not deny that active inhibitions are present whenever muscles have a particular autonomy or a particular tonus, as is the case with the muscles of the heart, blood vessels, and intestines. Here, indeed, there are special inhibitory nerves whose excitation causes an inhibition of the end organs in the muscles.

We have now seen some of the difficulties in the way of the centre theory, and also the theoretical character of the explanation offered by Goltz. It remains to speak of another explanation no less theoretical than the latter, but sharing with it a very generous share of popular approval.

*The Theory of Lauder Brunton.* To say that all inhibitions are due to the fact that the central nervous system does not permit its different parts to be simultaneously excited by different stimuli, leaves us in uncertainty as to how the nervous system comes to have such a property. An interference in the nerves themselves has accordingly been suggested. The first great exponent of this theory was Lauder Brunton. In its earlier stages his explanation was about as follows.<sup>2</sup> The excitation following a weak stimulation is carried only to a motor cell and produces movement. A strong stimulation passes over to an inhibitory cell whose activity cancels that of the motor cell, wholly or in part. This, however, did not suggest the doc-

<sup>1</sup> Verworn: *Zur Phys. d. nervösen Hemmungserscheinungen Arch. f. Anat. u. Phys.*, pp. 105 ff. Suppl. Abth., 1900.

<sup>2</sup> Brunton: *West Riding Asylum Reps.*, 1874, pp. 179-222. See *Nature*, Vol. 27, p. 437.

trine of interference, because Munk had shown that in different nerves the rates of transmission are different, and interference cannot be used as an explanation unless the rates of transmission are the same. Later it came to be believed that under like conditions the rates are similar, and Romanes took a forward step in experimental physiology<sup>1</sup> which led Brunton shortly afterward to state the theory we are about to discuss.

Romanes' experiments consist in tests on a strip of Medusa tissue at one end of which is a single lithocyst. He first observed the rhythm of activity of this lithocyst and then at the same rate stimulated the other end of the strip by electricity. The waves then always passed from the stimulated point toward the lithocyst. But if the rate of stimulation fell below that of the lithocyst, after one to six waves, depending upon the degree of conformity thereto, one passed in the opposite direction. When two such waves met they neutralized each other; or the tissue on each side of the meeting point, having lately been excited, could not transmit another excitation. The facts of inhibition then are explained as due to an interference of vibrations the rates of which are not synchronous.

Brunton now formulates the theory of interference on the analogy of the interference of waves of light and sound.<sup>2</sup> "Motion, sensation, inhibition, or stimulation are not positive but simply relative terms, and stimulating or inhibiting functions may be exercised by the same cell according to the relation which subsists between the wave lengths of the impulses travelling to or from it, the distance over which they travel, and the rapidity with which they are propagated."

The test of this theory is to be found, according to Brunton, in those variations of the conditions of temperature, etc., which change the rate of transmission in the nerves.

The effect of warmth or cold on strychnine tetanus, says Brunton, is what we should expect on the theory of interference. If small doses of strychnine are given warmth abolishes the convulsions but cold increases them; the contrary follows when large doses are given. The explanation he gives is in detail as follows: "If a small dose of strychnine retard the transmission of nervous impulses so that the inhibitory wave is allowed to fall more than half a wave length, but not a whole wave length behind the stimulus wave, we should have a cer-

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<sup>1</sup> Romanes: On the Locomotor Systems of Medusæ, *Philosoph. Trans.*, 1877, pp. 659-752. See Gen'l Summary, pp. 745 ff.

<sup>2</sup> Lauder Brunton: On the Nature of Inhibition and the Action of Drugs upon it. *Nature*, 1883, Vol. XXVII, p. 422. See the series of articles under this subject; same volume, pp. 419 ff., 436 ff., 467 ff., 485 ff.

tain amount of stimulation instead of inhibition. Slight warmth by quickening the transmission of impulses should counteract this effect and remove the effect of strychnine. Cold, on the other hand, by causing further retardation should increase the effect. With a large dose of strychnine, the transmission of the inhibitory wave being still further retarded, the warmth would be sufficient to make the two waves coincide while the cold would throw back the inhibitory wave a whole wave length, and thus again, abolish the convulsions."

Several other facts are offered by Brunton in favor of his theory. There is the well known phenomenon of accelerated heart activity during the act of swallowing because a part of the stimulus of the bolus, in the pharynx, passes to the centre in the medulla oblongata which is close to the root of the vagus. This nerve itself is inhibited and the heart works more rapidly. Stimulation of the sciatic nerve in a frog may inhibit the reflexes on the other side. A few hours later when conditions may be supposed to have changed, instead of inhibited response we find clonic convulsions. In the frog heart, according to the description given by Beale, Brunton finds a mechanism fitted for altering the distance two stimuli have to travel and thus allowing them to interfere with and to inhibit each other, and finally there is the observation of Mortimer Granville,<sup>1</sup> that by rapid percussion of a nerve already mediating a grinding pain, and by slow percussion of one mediating acute pain, he is often able to cancel the discomfort.

If we could be absolutely certain of that of which Mercier seems so confident,<sup>2</sup> viz.: that "nerve currents are known to be undulatory in form," and if we could be sure that, as he says, and as Loeb somewhere affirms, along every nerve fibre gushes of nerve force succeed each other as waves of blood in arteries and veins, we could more easily conclude in favor of this theory of inhibition by interference. Doubtless, as Herrick says,<sup>3</sup> it is the most generally accepted theory. But in the face of the fact that Wundt declares that there is no evidence for it,<sup>4</sup> and J. Kron, after an elaborate series of investigations in Mendel's laboratory,<sup>5</sup> comes to the conclusion that inhibitions are due to the changes in the supply of blood to the nervous centres, it is probably safer to do as so many others have done

<sup>1</sup> Mortimer Granville: *Nerve Vibration and Excitation*. London, 1883. See *Nature*, Vol. XXVII, p. 437.

<sup>2</sup> Mercier: *The Nervous System and the Mind*, p. 74.

<sup>3</sup> Herrick: *Baldwin's Dict. of Philos. and Psychol.* Art. *Inhibition*.

<sup>4</sup> Wundt: *Physiol. Psych.*, Bd. I, 1902, p. 87.

<sup>5</sup> J. Kron: *Experimentelle Beiträge z. Lehre von d. Hemmung d. Reflexe nach halbseitiger Durchschneidung d. Rückenmarks*. *Deutsche Zeitsch. f. Nervenheilkunde*, 1902, Bd. 22, Dec. Heft.

before, that is, to leave the question open for further investigation.

### III.

#### THE PHENOMENA OF SUMMATION.

Closely allied with the phenomena of inhibition are those of summation. If the recent prevailing views concerning these functions are correct one may almost say that they represent opposite faces of the same phenomenon. The summation of stimuli, true to the etymological significance of the phrase, is a heaping up of impulses. Every one is familiar with the extreme exasperation to which one may be driven by a fly which persists in attacks upon one's forehead, and with what vigorous gestures we seek once for all to annihilate the offender. An experience scarcely less well known is the irritation caused by a small body fast within the throat. First we cough slightly, then violently, and finally, if the offense continues, we fall into a cramp and emerge therefrom in a weakened, breathless state.

At the beginning of our half century of physiological history summated stimuli were little understood, and had not been specially examined.

Helmholtz<sup>1</sup> early gave a clue as to how these phenomena might be explained in calling attention to the slow rate of transmission from the sensory to the motor roots in the cord. (Exner's "reduced reflex time."<sup>2</sup>) He estimates that this transmission required from  $1/30$  to  $1/10$  sec., a much slower rate than that of impulses in the nerve fibres. This may be taken in connection with the early observation by Schiff on frogs, that the thinner the gray matter of the cord was made between the sensory and motor roots in the single locality tested, the longer is the reflex time.<sup>3</sup>

These facts suggest the crowding of impulses into a narrow passageway, or into a channel which offers some resistance, the later thus overtaking the earlier and heaping up upon them until of their own accumulated energy they break through *en masse*, pass over to the motor roots and occasion violent movement. The early methods of investigation, however, were inadequate to furnish any very reliable information regarding the time that must elapse between the application of a stimulus and its motor effect, or concerning the relations of interval and stimulus number best suited to optimum results. Setschenow showed that ability to summate stimuli belongs in an especially

<sup>1</sup>Helmholtz: Ber. d. k. Akad. d. Wissensch. z. Berlin, pp. 329 ff., 1854

<sup>2</sup>Exner: *Pflüger's Archiv.*, 1874, Bd. VIII, pp. 526 ff.

<sup>3</sup>Schiff: *Lehrb. d. Physiol.*, 1858-1859, p. 228.



high degree to the locomotor centres;<sup>1</sup> and that if a galvanic current be interrupted sixty times per minute, the reflex quiver occurs in a slight degree after the first interruption, and is confined to a limited number of muscles; the second, third, etc., interruptions are followed by more intensive and extensive contractions until a movement of the whole extremity follows. These experiments were with electrical stimuli. But Türck<sup>2</sup> much earlier and Baxt<sup>3</sup> somewhat later obtained the same result with chemical stimuli, and the latter set forth his law that the reflex time increases in geometrical progression while the degree of acidity of the stimulus decreases in arithmetical progression. Such a stimulus, he says, can occasion excitation only if its particles follow one another into the nerve tissue more rapidly than excitation passes away.

But the difference in the rates of transmission of different parts of the nervous system and the observation made by Schiff mentioned above did not open a way in the minds of all for the explanation. One of Schiff's own contemporaries accounted for the phenomena on the ground of the increased excitability of nervous tissue<sup>4</sup> and thought that this excitability can be measured by the position of the secondary coil required to produce a reflex as two, three, or four times a former excitability. Heidenhein in the same year found that muscle in a state of contraction is more excitable than at other times. Gruenhagen, however, denies that the phenomena in question are due to an increased excitability of muscular tissue or of any other tissue.<sup>5</sup> Pflüger had declared that during the process of death the positive forces of inhibition vanish more quickly than the forces of molecular tension. Hence when a stimulus is applied, in the absence of inhibitory forces, the nerve *appears* to have a heightened excitability. Harless, further, showed in a later work than that mentioned above that the simultaneous stimulation of two parts of the same nerve acts more strongly than a single stimulation of one part.<sup>6</sup> This, says Gruenhagen, is easily established.<sup>7</sup> The upper part of a nerve is more excitable than the lower as can be easily shown by the comparison of the effects of two electrical stimuli one passing up, the other down the nerve. No less plausible, thinks Gruenhagen, is Pflüger's

<sup>1</sup>Setschenow: Monog. über d. elec. u. chem. Reizung d. sensib., Rückenmarksnerven d. Frosches, Gratz, 1868, I, sec. 12, u. a.

<sup>2</sup>Türck: *Zeitsch. d. Gesell. d. Aerzte*, 1850, H. III.

<sup>3</sup>Baxt: Arbeiten aus d. phys. Anstalt z. Leipzig, 1871.

<sup>4</sup>Harless: Ueber Muskelzuckungen bei dem Vertrocknen d. Nerven. München, Gelehr. Anz., XLVIII, 1859, col., 241-246.

<sup>5</sup>Gruenhagen: Bemerkungen über d. Summation v. Erregungen in d. Nervenfasern. *Zeitsch. f. rat. Med.*, pp. 190 ff. XXVI, 1866.

<sup>6</sup>Gruenhagen: *op. cit.*

<sup>7</sup>Gruenhagen: *op. cit.*

decision that in the absence of inhibitory forces nervous tissue possesses only apparently a higher degree of excitability than formerly. Gruenhagen assumes that in an animal in which the lower and higher nervous centres have been separated, the moisture contained in the nerves begins to evaporate. This process occasions more or less of a crumpling or folding of the nerve masses, and this in turn a stimulation of the fibres which, within certain limits, is the more intense the further the process of evaporation has proceeded. Any peripheral stimulus produces an excitation which is added to this aroused internally, and a more vigorous contraction attends a weak peripheral stimulus than, in a fresh state of the nerves, accompanies a much more intense external stimulus. Gruenhagen thus arrives at a conception of summation. Pflüger had shown that of two frog shanks one stimulated from the plexus, the other from the muscle itself, the former is the more quickly thrown into contraction. This, he explains, on the assumption of an avalanche-like swelling of excitations as the excitement of the plexus proceeds toward the muscle. Gruenhagen, however, prefers, in this connection, to speak of a rolling up of nerve force.

Previous to 1874 no very systematic work had been done on this subject. In that year, however, William Stirling published his work on summation<sup>1</sup> in which the phenomena described are discussed in detail. In none of the tables which he presents is any relation whatever to be found between the intensity of the stimuli and the time of latency. This much controverted point has been confirmed in our own times by Goldscheider. But latency does depend invariably, as Stirling shows, upon the frequency with which stimuli follow one another. Though it varies somewhat according to the part of the body as well as with the animal on which tests are made, *e. g.*, Tigerstedt shows that 27 stimuli per second produce tetanus in the gastrocnemius of the frog while 10 per second have the same effect on the red muscle soleus in the puppy. Other things equal, the shorter period of latency always accompanies the shorter stimulus interval. It is inadmissible to compare the results of several experimental series with one another even though the stimulus interval be uniform throughout for the reason that at different stages in the life of a preparation these periods vary considerably from causes which we cannot compute. For instance, with a constant interval of  $\frac{1}{8}$  second variations in latency in a series of experiments may occur between .5 and 5 seconds: with an interval of  $\frac{1}{4}$  second the variations

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<sup>1</sup> Wm. Stirling: *Summation v. elec.*, Hautreizen, Ber. d. sächs. Acad. Math. phys., 1875, pp. 372 ff.

range from 1 to 30 seconds. As the interval increases above the optimum he shows, in analogy with Baxt's law, that the number of stimuli necessary for producing a contraction must surpass by many fold those required where a shorter interval is used.

Can any reflex movement occur without a summation of stimuli? All agree that much greater intensities of currents are required for the production of reflexes by a single stimulus than in the classical summation experiments in which a series of relatively weak stimuli are used. To find the cause of this difference Stirling compared in many ways the effect of single induction shocks with that of repeated stimuli. All apparently spontaneous movements of reflex animals he was led to put down, incidentally, to the account of summation.

To the objection that demonstrably simple stimuli may produce effects such as are attributed to summation, Engelmann replies<sup>1</sup> that very intense induction shocks produce chemical and thermal variations in the substance of the nerves, and Stirling has observed that a sensitive frog shank, with a single shock, is often thrown into tetanus. He would, therefore, bring single stimuli into the sphere of summation, and state it as a general law that reflexes can be called out only by repeated stimuli.

The problems of summation were later carried into a field of more immediate interest to the psychologist. Recent studies furnish some evidence of a connection of summation with sensation. Naunyn in his study of the sensation of pain<sup>2</sup> has found that under the conditions observed in summation experiments in general the period of latency of pain summation is the same as that of the summation of sensory stimuli for the production of reflex movements. This, however, as Naunyn recognizes, does not establish the matter beyond a doubt but only makes it probable that pain is a product of summation.

Goldscheider brings the "secondary sensation" into relation with the summation of stimuli.<sup>3</sup> If one's skin is pricked with a needle, after a sensationless interval an after-sensation appears which, though of varying degrees of clearness, cannot be mistaken. In the course of his experiments he found that there is no definite relation between stimulus number and stimulus interval: different intervals are favorable for a clear after-sen-

<sup>1</sup>Engelmann: *Bewegungserscheinungen an Nervenfasern bei Reizung mit Inductionsschlägen*. *Pflüger's Arch.*, Bd. V, pp. 31 ff.

<sup>2</sup>Naunyn: *Ueber d. Auslösung v. Schmerzempfindung durch. Summation sech zeitlich folgender sensiblen Erregungen*. *Arch. f. exper. Pathol. u. Pharmakol.*, Bd. XXV, pp. 272 ff.

<sup>3</sup>Gad and Goldscheider: *Summation v. Hautreizen*, Bd. I, *Gesammelte Abhandlungen*, pp. 397 ff. Leipzig, 1898.

sation at different times with the same number of stimuli. This variability, however, belongs only to a limited sphere. If the number of stimuli is large the variations of intervals must be slight. If the intervals are long the number of stimuli for optimum results must be almost constant. Goldscheider formulates the following law: "With increasing stimulus interval the number of single stimuli required for clearness of secondary sensation decreases: with decreasing interval the stimulus number must increase." The latency time of the after-sensation depends less upon the kind and intensity of stimuli than upon the velocity with which they succeed one another. In this respect the after-sensation is similar to the reflex movement produced by the summation of sensory stimuli.

While Goldscheider's explanation is on the ground of summation his scheme is somewhat different from that of those who attribute the phenomena of summation and inhibition to the interference of waves of excitation or of nerve force within the nerves themselves. For him the gray matter of the cord is the summation tract. When an excitation arrives from the periphery a part is transmitted directly to the centre of consciousness and a part to the cells in the gray matter described by Kölliker.<sup>1</sup> In these cells he supposes a change in the state of excitability. The excitation is stored up here to be discharged later and transmitted to the centre of consciousness when it is recognized either as pain or as a secondary sensation of the same quality as the primary.

#### IV. VASCULAR TONUS.

As we saw in Section I the conception of a reflex vascular tonus originated in 1852 with Claude Bernard who discovered the vaso-constrictor fibres, by the immediate influence of which the walls of the blood vessels were supposed to be kept in a tense condition. A few years later Schiff believed that he had demonstrated the presence of vaso-dilator fibres in the cervical sympathetic of a rabbit<sup>2</sup> and again Bernard somewhat later believed he had still more conclusively demonstrated their existence. But with this the question was not decisively settled and it has been discussed pro and con until the present time when McKendrick asserts his belief in some sort of inhibitory mechanism which accounts for the dilation of the vessels,<sup>3</sup> and Dastre and Morat, Howell and Porter find for interference with peripheral ganglionic mechanisms, and for antagonistic fibres

<sup>1</sup>Kölliker: Ueber d. feinern Bau d. Rückenmarks, Sitzungsber. d. phys. med. Gesells. z. Würzburg, 1890, p. 40.

<sup>2</sup>Schiff: Berner Schriften, 1856, p. 69 ff.

<sup>3</sup>McKendrick: Textbook of Special Physiol., 1889, p. 296.

within the nerve trunks.<sup>1</sup> Until, however, these fibres of opposite function can be positively demonstrated, it is simpler and more satisfactory, if we must take sides, to give preference to the theory of Dastre and Morat, and thus bring the constriction and dilation of the blood vessels into analogy with the excitation to, and inhibition of, those reflexes which are more familiar to us.

Besides this question of constrictor and dilator fibres there was another of considerably greater interest to the physiologists of the early part of our half century. Such fibres once granted, from what anatomical points in the central nervous system is the vascular system controlled?

These were sought with great zeal in the spinal cord; and Schiff first clearly stated that the vascular centres are located in that part of the nervous system. It is hardly within the scope of this paper to enter into the anatomical details. Suffice it to say that Lister, Goltz, Owsjannikow, Ludwig, Gaskell, and others of no less repute, have throughout laborious years sought for regions of predominating influence upon the circulation of the blood, and that to-day, with the addition of some details, our knowledge of this matter is practically as Lister left it in 1858: in a word that the tonus of the blood vessels depends upon the cord and local ganglia.<sup>2</sup>

It is of more importance for our purpose to know whether these changes in vascular tonus are reflex or automatic.

The supposition of the reflex character of the vascular phenomena has much in its favor. The experiments which were made to demonstrate the existence of vaso-constrictor and vasodilator fibres point in that direction; but these are not all. It had early been observed that if one hand be immersed in cold water the temperature of the other falls from one to twelve degrees C. In many such cases the temperature of the mouth and axilla rises slightly indicating that the temperature of the body as a whole is not altered. This observation was originally made by Brown-Sequard. Later he and J. S. Lombard performed confirmatory experiments. Cyon also, in 1866, declared that he had proved that the vascular centre in the *medulla oblongata* can be influenced by impressions from the periphery, *i. e.*, in a reflex manner.

The experiments by Brown-Sequard and Lombard suggested more extensive tests which were made by Putnam on frogs in 1870.<sup>3</sup> These experiments are of importance because they

<sup>1</sup> Dastre: *Arch. d. Physiol. norm. et pathol.*, 1882, p. 190.

<sup>2</sup> Lister: *Philos. Transac's*, London, 1858, pp. 607 ff.

<sup>3</sup> J. J. Putnam: A report of some Experiments on the Reflex Contractions of the Blood Vessels. *Boston Med. Jour.*, Vol. LXXXII, 1870, pp. 469-472.

show so clearly the reflex function of the central nervous system in relation to the blood vessels. The web of one hind foot, after the removal of the *medulla oblongata*, was watched under the microscope while the other was stimulated mechanically and chemically. Contraction of the vessels on the side opposite the stimulation is not absolutely invariable, but sufficiently so after all causes of variation have been taken into account, to make the assertion safe that the phenomena fall under the category of ordinary reflexes.

Putnam's conclusions fall in with an observation made by Callenfels and confirmed also by O. Bezold. Callenfels says:<sup>1</sup> "If one cuts the spinal nerve (to the ear) in a rabbit, an operation which causes a slight dilation in the blood vessels in the ear of the same side, one can afterward provoke a contraction of these same vessels not only by galvanizing the peripheral end of the cut nerve, but also by irritating, in the same manner, its trunk which still remains in connection with the medulla, and which is no more in direct communication with the part where the effect is produced. It must be then that an irritation has been transmitted to the cerebro-spinal axis and has there set up a nervous action which is directed toward the vessels of the ear." In this case the reflex arc between the stimulated point on the central stump and the vascular area where the effect is produced, is composed of the central stump of the severed nerve, the cord or spinal ganglion and the sympathetic fibres leading from this centre to the walls of the vessels. Much later than this Moritz Nussbaum expressed his belief in the possibility "that many sensory nerves are able reflexly to widen the arteries directly through the excitation of inhibitory centres or the relaxation of vaso-motor centres."<sup>2</sup> Further he says that from his investigation "it follows that the vaso-motor centre extends through the cord into the *medulla oblongata* and can be set into heightened reflex activity by all sensory nerves."

But the matter is by no means a simple one, for vascular variations occur also in the absence of the entire central nervous system, as was early shown by Lister<sup>3</sup> and others, given a crucial demonstration by Gergens and Werber<sup>4</sup> and reconfirmed by Gley in 1844 and by Goltz and Ewald<sup>5</sup> in 1896.

It may now be asked: What are the stimuli—the first term of the reflex series—which in normal life provokes vascular

<sup>1</sup> Callenfels: *Zeitsch. f. rat. Med.* Bd. VII, 1855, p. 157.

<sup>2</sup> Nussbaum: Ueber d. Lage d. Gefässcentrums. *Pflüger's Arch.* X, 1875, pp. 374 ff.

<sup>3</sup> Lister: *op. cit.*, pp. 617 f.

<sup>4</sup> Gergens and Werber: *Pflüger's Arch.*, Bd. XIII, 1876, pp. 44-61.

<sup>5</sup> Goltz and Ewald: Der Hund mit verkürztem Rückenmark. *Pflüger's Arch.*, Bd. LXIII, 1896, pp. 362-401.

tonus and the variations in the lumen of the vessels? It must be answered that they cannot be pointed out with certainty. Not a few of the older investigators preferred indeed to escape the need of pointing them out by calling the control automatic, though the present tendency is toward a reflex explanation, with considerable variety of opinion as to just what the stimuli are and just how they are applied.

Taking the tonus question as a whole, we see in the course of the investigations that from simple beginnings the conception of a complicated reflex mechanism has been developed. Early in the period there was a tendency to consider the vascular centres automatic, but as knowledge of the effect of both external and internal stimuli has increased the automatic theory has been given up, and co-ordinately with the growth of the reflex idea has risen also the idea of the importance of the entire organism in vascular control as opposed to that of any particular parts.

## V. MUSCULAR TONUS.

In the first section of this paper it was pointed out that the early physiologists represented by Müller and Henle had, with some exceptions, including Ed. Weber, declared their belief in a muscular tonicity dependent upon the central nervous system. Such a tonus they, as we to-day, defined as a permanently contracted state of the muscular fibres. One's characteristic physiognomy, which in popular thought is supposed to have a psychic substrate, they attributed to the state of tonus of the facial muscles. This was Henle's idea. But Wundt, much later, in a brief period of reaction from the tonus theory, declared that this can be more easily explained on the ground of temperament and the fact that the muscle substance is not completely elastic.<sup>1</sup>

In the later 50's the question whether there is a muscular tonus independent of mere muscular elasticity was in an unsettled state. Nor was such a term generally accepted by physiologists in the description of muscular phenomena until much later. By exact measurement Heidenhain,<sup>2</sup> in 1856, failed to find any lengthening of muscles after their nerves had been cut, neither did Auerbach in the same year.<sup>3</sup> In the face of this negative evidence, offered by men of such authority in physiology, who were two years later reinforced by Schiff,<sup>4</sup> the

<sup>1</sup>Wundt: *Muskelbewegung*, 1858, pp. 45 f.

<sup>2</sup>R. Heidenhain: *Hist. u. Exp. über Muskeltonus*. *Physiol. Studien*, Berlin, 1856, p. 19 ff.

<sup>3</sup>Auerbach: *Ueber Muskeltonus*, *Jahresb. d. schles. Ges. f. vaterl. Cultur*, 1856, pp. 127 ff.

<sup>4</sup>Schiff: *Muskel. u. nerven Phys.*, 1858, pp. 30 ff.

phrase "muscular tonus" was fairly on its way to oblivion. "Certainly," says Wundt, "in the natural sciences we may explain phenomena by analogy with others better known. But when the number of natural forces is increased by way of explanation we are justified in mistrust and in criticism especially when no convincing proof is adduced for the creation. In the case of muscular tonus such proof is by no means furnished. We can explain the tense state of muscles without going beyond what we know to exist."<sup>1</sup> The constant tension of muscles, he is convinced, can be explained by elasticity.

But the fundamental experiment was yet to be made. This was performed by Brondgeest in 1860.<sup>2</sup> Though his earlier experiments had led him to negative results, the one in question he thought required the assumption of a muscular tonus. The sciatic nerve on one side of a spinal frog was severed and the animal was suspended by the jaw. At once the foot on the opposite side was found to form the greater angle with the median line of the body. Furthermore he concluded that this tonus is a reflex since section of the posterior roots produces precisely the same phenomena as severing the sciatic.

This work of Brondgeest's called forth many repetitions of the experiment in different forms. Hermann assumes a spinal sensorium.<sup>3</sup> The frog is trying to hold his foot up in its normal position when at rest and he "holds it at such a height as he can endure without exhaustion."

Cohnstein observed that a frog prepared according to Brondgeest's method, and placed in a horizontal position upon a surface of quicksilver shows no difference whatever in the position of its limbs.<sup>4</sup> Brondgeest's tonus is therefore due, he thinks, to the stimulus afforded by the traction of the muscles upon the skin. It is a reflex: not necessarily a constant state of the muscles in the sense of Müller and Brondgeest. Neither is it necessarily uniform all over the body. Here a group of muscles may be tense, there another flaccid. The difference between this explanation and that offered by Lombard in 1896 is only a matter of words.<sup>5</sup> Lombard says: "If, when one is quietly sitting, one turns one's attention to the sense impressions coming from clothes, warmth, sight, hearing, one is convinced of the multitude of impressions exciting the nervous

<sup>1</sup>Wundt: *Muskelbewegung*, 1858, p. 45.

<sup>2</sup>Brondgeest: *Arch. f. Anat. u. Physiol.*, 1860, pp. 703 f.

<sup>3</sup>Hermann: *Beiträge zur Erledigung d. Tonusfrage. Arch. v. DuBois u. Reichert*, 1861, pp. 350 ff.

<sup>4</sup>J. Cohnstein: *Kurze Uebersicht d. Lehre vom Muskeltonus. DuBois u. Reichert's Arch.*, 1863, pp. 165 ff.

<sup>5</sup>Lombard: *Art. Am. Text B. of Phys.*, 1896, p. 134 ff.



system. The effect of all this is to cause motor cells to send delicate excitations to the muscles. Hence muscular tonus." Yet more convincing than any other argument for the negative was that which Schwalbe proposed after a long series of experiments.<sup>1</sup> Brondgeest's phenomena, he says, are due to an increased elasticity of muscles which remains behind after vigorous action and only gradually passes away. These experiments led G. Heidenhain, in 1871, to think the whole question of muscular tonus ended. And Eckhard, too, in 1879, doubted its existence. This, however, was a mistaken position.

The evidence on the positive side of the question is really preponderant and, Ferrier says,<sup>2</sup> in speaking of the work of Cyon and Tschirjew: "The negative results of previous experiments must, therefore, be attributed to faulty methods, and the existence of a muscular tonus, of a reflex character at least, must be considered as proven." Cyon, in 1865, showed that the excitability of the motor roots is heightened by stimulation of the sensory,<sup>3</sup> and several years later confirmed by exact measurement<sup>4</sup> the results of Steinmann who found that section of the posterior roots is followed by lengthening of the muscles. A little later Tschirjew demonstrated the same phenomena with equal exactness.<sup>5</sup> Thereafter there were a few isolated attempts to disprove the theory, and some investigators even in the face of these accurate scientific measurements continued to doubt; but it was not quite in accord with the facts when, in 1887, Westphal said that at that time physiologists were not inclined to admit the existence of a muscular tonus. At the present time the consensus is general in favor of the tonus theory.

Let us now turn to the question of how the tonic state is maintained. The arguments for an automatic tonus have not received very extended consideration though Foster says<sup>6</sup> that "it seems a matter of words whether we speak of it as an automatic or a reflex action of the cord. We may distinguish the part played by an afferent impulse in maintaining tonus from the part played by it in causing reflexes. In the former it is analogous to a supply of arterial blood in maintaining an adequate irritability of nervous substance. In the latter the impulses lead directly to a discharge of energy. And it is con-

<sup>1</sup>Schwalbe: Pflüger's Untersuch. aus d. Bonner phys. Lab., 1865, pp. 64 ff.

<sup>2</sup>Ferrier: Functions of the Brain, 1886, p. 82.

<sup>3</sup>Cyon: Ber. d. sächs. Ges. d. Wissensch. Math. Phys. Cl., 1865, Bd. XVII, pp. 85 ff.

<sup>4</sup>Cyon: Pflüger's Arch., Bd. VIII, 1874, pp. 347 ff.

<sup>5</sup>Tschirjew: Arch. f. Anat. u. Phys., 1879, pp. 78 ff.

<sup>6</sup>Foster: Textbook of Phys., Vol. III, p. 925, 1892.

venient to call the two by different names." It is, however, conceded that the tonus of the muscles of the blood vessels and the sphincters is automatic.

That muscular tonus, especially of the skeletal muscles, can be affected reflexly does not admit of a doubt. Sherrington cut the nerve leading to the hind leg of a cat.<sup>1</sup> When he stimulated the central stump the tonus of the extensor was lowered and the lower shank hung down straight. This phenomenon comes under the formula for reflex actions involving the spinal axis. Wundt says:<sup>2</sup> "The tonic excitations of the skeletal muscles appear to be of an exclusively reflex nature, since section of the muscle nerves aside from the accompanying quivering and elastic after-effects produces no change of muscular tension." But the arguments for automatism aside, and the reflex nature of the phenomena once granted, the question remains as to the organs mediating the stimuli for arousing the reflex.

As stated above Cohnstein in 1865 believed that the stimulus is afforded by the traction of the skin by the weight of the muscles. This theory for a long time received the most complete acceptance. But even where the skin lies in loose folds, without any tension whatever under the weight of the muscles, the latter are in a state of tonus. Experiments on frogs have proved that large portions of skin may be removed from the body without prejudicing muscular tonicity, or even interfering with co-ordinated movement which is so much under the influence of the tonicity of the muscles.

Mommsen, in 1885, reviewed arguments and experiments to show that the constant tension of the muscles is not, as Eckhard says,<sup>3</sup> entirely dependent upon afferent cutaneous impulses.<sup>4</sup> That afferent roots, however, have a function in connection with the phenomena in question, is beyond a doubt. The blocking of all afferent channels in a limb lowers the tonus of its muscles. Such a limb becomes excessively mobile and *rigor mortis* is delayed in its muscles.<sup>5</sup>

But how much of this result is due to the section of cutaneous afferent nerves cannot be determined. Since, as already stated, removal of an animal's skin does not cause tonus to cease entirely this state must be due in part to influence from the mus-

<sup>1</sup>Sherrington: On Inhibition of the Tonus of a Voluntary Muscle by Stimulation of its Antagonist. *Jour. of Physiol.*, Vol. XXIII, Suppl. 1898, p. 26.

<sup>2</sup>Wundt: *Physiol. Psych.*, Bd. II, 1902, p. 254.

<sup>3</sup>Eckhard: *Hermann's Handb. d. Phys.*, Bd. II, pp. 269 f.

<sup>4</sup>Mommsen: *Beitrag z. Kenntniss d. Muskeltonus*. *Arch. f. Path. Anat. u. Phys.*, Bd. 101, pp. 22 ff.

<sup>5</sup>Sherrington: Schäfer's *Phys.*, Vol. II, p. 799.

cles. Tschirjew, whose work in connection with Cyon's is so important for this subject,<sup>1</sup> called attention to the fine network of intrafibrillar nerves within the muscles, and believes that these are the end organs for muscular tonus, and the centripetal nerve fibres of the muscles. The stretching of these fibres by the weight of a dependant limb, their compression by the muscles, or their disturbance by the activity of the muscles, he thinks, furnishes the stimulus for reflex tonus. Tschirjew relates some experiments with dogs in support of his theory. Such an animal is put upon his back so that his legs of their own weight are bent upon his body. The limbs are soon found to be asleep: *i. e.*, the muscles are toneless. Like phenomena under similar circumstances can be observed in men. This, Tschirjew attributes to the quiet unstretched condition of the muscles so that the nerve fibres in the aponeuroses are undisturbed.

It is impossible to demonstrate that either muscle or skin has a controlling interest in the production of tonus. By co-cainization or flaying the effect of cutaneous impressions can be ruled out, but it is not possible to dispose of the muscular nerves while leaving the muscles intact.

## VI. TENDON REFLEXES.<sup>2</sup>

Closely related to muscular tonus are the tendon reflexes. In its absence they do not appear. Hence the production of knee jerk is a practical means for demonstrating the tension of muscles.

Scarcely three decades have elapsed since these phenomena were first described, but their great practical importance in the diagnosis of certain spinal diseases justifies the voluminous literature of a descriptive and experimental character which has appeared in this field within so brief a period. The tendon reflex is rarely absent in health but it is entirely abolished in tabes dorsalis, locomotor ataxy, and atrophic paralysis, and increased in diseases of the lateral columns. Further it has been supposed<sup>3</sup> that these phenomena have much influence in the purposeful management of movements, and that in men they are of importance in the maintenance of equilibrium.

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<sup>1</sup> Tschirjew: *op. cit.*

<sup>2</sup> For the material of this section I am largely indebted to the exhaustive account of the subject found in Hermann Netter's Inaug. Dissert.: "Geschichte d. Lehre vom Knie-phänomen." Freiburg, 1897. The citations herein, excepting where exact page references are given, are *copied directly from Netter's work.*

<sup>3</sup> Saureys: Quelques réflexions sur le raison physiologique et la localisation probable du réflexe patellaire. Ref. Annales de la Soc. Belge de Neurol. V<sup>e</sup> année.

The knee jerk, produced by smartly striking the patellar ligament of a dependent limb, is a typical instance of the phenomena. On such a stimulus the lower leg is involuntarily thrown forward. The jerk is by no means confined, however, to the knee. It may be produced by a similar stimulation of any ligament in the body.

The phenomenon was first described by Erb<sup>1</sup> who believed that it was a true reflex, analogous to those excited by cutaneous stimulation, and dependent upon an entire reflex arc. Tschirjew was the first to investigate it experimentally, and he, too, decided in favor of the reflex theory.<sup>2</sup> Westphal, however, looked upon it as a direct muscular contraction induced by the sudden tension occasioned by the blow upon the tendon.<sup>3</sup> Erb and Westphal, therefore, represent opposite poles of thought on this question and about them many supporters have rallied. The disciples of Westphal are found chiefly among English and American scientists, those of Erb among the Germans. Erb and Westphal were of the same opinion only in this,<sup>4</sup> that the tendon phenomena do not depend upon cutaneous impressions.

We shall first speak of the supporters of Erb and the reflex theory. Tschirjew has already been referred to as a member of this school, and the first experimental investigator of the tendon phenomena.<sup>5</sup> He found that the knee jerk disappears when the cord is cut transversely between the fifth and sixth lumbar vertebræ in puppies. This observation was later confirmed by Senator who found that hemisection of the cord displaces the phenomena only on the side of the cut.<sup>6</sup> Another indication, from the standpoint of the anatomist, of the reflex nature of the knee jerk is found in the fact, to which Sachs called attention, that the tendons themselves contain nerves.

But more convincing than any anatomical evidence are the experiments by Schultze and Fürbringer, who published their work in 1875. In one experiment on puppies the cord was cut in the upper dorsal region and the quadriceps muscle was severed from the patella. The disconnected muscle was then held above the bone, so as not to be affected by its jarring, and slightly stretched. It responded, by slightly twitching, to every stroke upon the opposite patellar ligament, but after either left or right crural nerve was severed the phenomenon

<sup>1</sup>Erb: *Arch. f. Psychiatrie*, Bd. II, 1875.

<sup>2</sup>Tschirjew: *Arch. Psychiatrie*, Bd. VIII.

<sup>3</sup>Westphal: *ibid.*, Bd. V.

<sup>4</sup>Tschirjew: *op. cit.*

<sup>5</sup>Tschirjew: *op. cit.*

<sup>6</sup>H. Senator: Ueber Schnenreflexe u. ihre Beziehungen z. Muskeltonus. *Arch. f. Anat. u. Physiol.*, 1880, pp. 197 ff.

could no more be produced in any way. Their conclusion is that in the tendon phenomenon we have not to do with a mechanical muscular contraction mediated directly through the tendons, but with a reflex mechanism whose arcs for the lower extremities pass through the lower parts of the cord. Gowers, Buzzard, Prevost and others also have decided in favor of the reflex theory, and Sternberg, in a series of articles,<sup>1</sup> makes the evidence practically decisive. He shows that a muscle may be severed from its ligament, lifted from the bone and turned back into a reversed position without influencing the tendon phenomenon.

Of another nature are the experiments by Tschirjew, Rosenheim and others. They measured the time of latency between stimulus and knee jerk and compared it with the latency period in recognized reflexes and in direct muscle stimulation. The time measured by Tschirjew is too long to lend color to the theory of direct muscle stimulation, and Rosenheim<sup>2</sup> never found a shorter period than .025 second: this and even greater periods corresponds to the latency times of undoubted reflexes. Rosenheim further computed the distance from the knee to the spinal cord and concluded that the latency time found by him is about such as should be expected under the conditions of an ordinary reflex.

Of the same character as these are a number of experiments performed by A. D. Waller which are construed as support for Westphal's theory of direct muscle stimulation.<sup>3</sup> He found that the latency time of the knee jerk in men is about .03 seconds, which, he says, is so much shorter than the latency of a true reflex that this phenomenon must be considered a result of direct muscle stimulation. But since the latency of the lid reflex is only .05 seconds (Exner) the difference is hardly sufficient to be convincing. Of more significance for this theory are his experiments on puppies. With direct electrical stimulation of the *rectus femoris* the latency time is .0076 second. The tendon phenomenon of the same muscle is .008 second, while the time between a cutaneous stimulus and a true reflex he gives as .033 second. Obviously the meaning of this comparison depends upon the place and conditions of cutaneous

<sup>1</sup> Sternberg: Sehnenreflexe bei Ermüdung, *Centbl. f. Phys.*, 1887; ditto: Ueber Sehnenreflexe, *Verhandl. d. Cong. f. innere, Med.*, 1890; ditto: Monogr. Die Sehnenreflexe, etc., Leipzig, u. Wien, 1893.

<sup>2</sup> Rosenheim: Exper. Unters. d. unter den Namen "Sehnenphänomene" bekannten Erscheinungen unter möglichsten Berücksichtigung vom Versuchen am Menschen u. patholog. Unters., *Arch. f. Psychiatrie u. Nervenheilk.*, XV.

<sup>3</sup> Waller: On the physiol. Mechanism of the phenomena termed "Tendon Reflexes." *Jour. of Phys.*, XI, pp. 384 ff.

stimulation. In another communication<sup>1</sup> he compares the distance of the gastrocnemius and rectus from their spinal centres as  $\frac{1}{2}m - 1m$ . The delay in the peripheral nerve, therefore, according to his computation, if the phenomenon is a reflex, should be .02-.03 second and .04-.06 second, plus the central and muscular latencies. As a matter of fact, however, they are about the same: .03-.04 second. De Watteville also argues for the direct stimulation theory on the ground of difference in latency times.<sup>2</sup>

It is unnecessary to go into the details of other analogies between the tendon phenomena and recognized reflexes. Suffice it to say that Sterling and Kronecker, Rosenheim, Jarisch and Schiff<sup>3</sup> all find that the knee jerk is subject to the law of summation of minimal stimuli and that Prevost and others have produced the crossed phenomenon.

The reflex theory, indeed, is in so general favor that we may fairly cease speaking of "tendon phenomena" and substitute therefor "tendon reflexes."

#### VII. DIRECTION OF TRANSMISSION AND CO-ORDINATION OF REFLEXES.

It was pointed out in the first section of this study that Pflüger's Laws represent the last important stage in the development of our knowledge of reflexes in the period previous to that which we are reviewing.<sup>4</sup> It is now our task to see how these laws have stood the test of fifty years and in connection with them to introduce some other matter of wider general interest.

The laws were for a long time generally accepted. But there are exceptions to each of them and in the light of present knowledge they hardly merit the importance that has been given to them. The contraction of muscles does not always occur on the side of the stimulus. It often occurs on the opposite side, depending upon the intensity of the stimulus—a contradiction of the first law. It is not always true that a unilateral reflex, if it spreads, involves the symmetrical opposite muscles. In the course of numerous experiments on dogs, Goltz was impressed with the vigor with which diagonally crossed reflexes occur after the cord has been separated from the inhibitory influence

<sup>1</sup>Waller: Muscular Symptoms known as Tendon Reflex. *Brain*, Vol. III, pp. 179 ff.

<sup>2</sup>de Watteville: On Reflexes and Pseudo-Reflexes., *Brit. Med. Jour.*, May 20, 1882.

<sup>3</sup>Jarisch u. Schiff: Unters. über d. Kniephänomen. *Weiner med. Jahrb.*, 1882.

<sup>4</sup>A statement of these laws is given by Dr. Hodge in his sketch of the earlier history of reflexes. *Am. Jour. of Psy.*, Vol. III, pp. 359 f.

of the brain.<sup>1</sup> Gergens also, working with dogs, found the same crossed phenomena.<sup>2</sup> If the left side of a spinal dog's neck be lightly tickled the right hind leg performs scratching movements. This phenomenon is invariable under these conditions with dogs. That it is independent of any volitional activity on the animal's part is indicated by the fact that however vigorous are the scratching movements the animal appears totally indifferent to them. Luchsinger added to these tests a number of experiments on tritons and lizards and substantiated the earlier observations.<sup>3</sup> With frogs, however, he was unable to induce a crossed reflex. Again the same author performed analogous experiments on the cricket and carabus, creatures with six legs.<sup>4</sup> These were painted with ether and thus made reflex. By the aid of a pair of tweezers he made walking movements with the middle leg on one side of the cricket and the diagonally opposite hind limb moved likewise. The carabus, which, unlike the cricket, uses all three pairs of legs for locomotion, under a like test on a front leg reflexly moves the diagonally opposite middle leg and the hind leg diagonally opposite the latter. On the other hand, says Sherrington, "in the spinal rabbit the crossed reflex from one hind limb to the other is not an asymmetrical movement but a symmetrical flexion."<sup>5</sup> This, as Luchsinger saw,<sup>6</sup> has its explanation in the normal mode of locomotion of the animal in question. Crossed reflexes in the locomotor organs occur in animals which propel themselves as the dog and cat; symmetrical reflexes in hopping animals such as the frog and the rabbit. There are thus exceptions to the second law.

The abduction of the tail from the point attacked, when it is intensely stimulated, is a well-known exception to the third law.

And as to the fourth law, viz.: that the spread of a reflex excitation is always toward the head if a spinal nerve is originally stimulated, there are numerous contradictions. The experiments, described below, made by Mendelsohn, show that irradiation may occur from the head tailward. On this point Sherrington says:<sup>7</sup> "From the pinna may be excited move-

<sup>1</sup>Goltz: Ueber d. Verrichtungen d. Grosshirns. *Pflüger's Arch.*, Bd. XIII, p. 1 ff.

<sup>2</sup>Gergens: Ueber gekreuzte Reflexe. *Pflüger's Arch.*, Bd. XIV, pp. 340-341.

<sup>3</sup>Luchsinger: Ueber gekreuzte Reflexe. *Pflüger's Arch.*, Bd. XXII, pp. 179-180.

<sup>4</sup>Luchsinger: Zur Theorie d. Reflexe. *Pflüger's Arch.*, XXIII, pp. 308 ff.

<sup>5</sup>Sherrington: Schäfer's Textbook of Phys., Vol. II, p. 822.

<sup>6</sup>*Op. cit.*

<sup>7</sup>Sherrington: Schäfer's Physiol., Vol. II, p. 823.

ments of all the limbs, the neck, the tail, and trunk. The irradiation from this reflexigenous area usually presents the following order: 1, Neck and homonymous fore limb; 2, homonymous hind limb; 3, tail and trunk on both sides; 4, contralateral hind limb; 5, contralateral fore limb. From the fore foot can be excited, besides movements of the fore limb itself, movements in the other limbs and tail." Recently there appeared a paper by the same author which grew out of a successful attempt to find detailed evidence of aborally running reflex spinal paths.<sup>1</sup> He found that "Each spinal segment (in the dog) possesses a wealth of neurones with backward running axons connecting it with practically all the spinal segments behind itself,"<sup>2</sup>—one more piece of evidence that the fourth law does not hold good in the mammalian spinal cord. With all this, however, especially in the case of the "long reflexes," it is difficult to predict the course of an excitation. Very often it happens that, for no reason that can be discerned, the usual course of dispersion of excitation is unused and an unusual one chosen.

It appears, therefore, that different portions of the cord are, as Rosenthal thought, differently suited to the transference of reflex excitations. But this investigator believed that normal reflexes are made possible chiefly through the mediation of the *medulla oblongata* and also through the uppermost parts of the cord. The exhaustive experiments by Mendelsohn sufficiently test the latter conclusion and furnish additional contradictory evidence regarding the validity of Pflüger's fourth law. In his first communication<sup>3</sup> he confirms Rosenthal so far as reflexes occasioned by weak stimuli are concerned. For the effectiveness of such stimuli the integrity of the upper part of the cord is necessary. Their effect is prejudiced if a cross section of the cord be made a few millimeters above the brachial plexus, or if a longitudinal median section is made from above to the same point. These statements apply only to the occurrence of reflexes on the side opposite the stimulus which is applied to a hind extremity. The upper part of the cord is therefore more open than the lower to the transmission of excitations. In the second communication<sup>4</sup> the author discusses the effects of hemi and total cross sections of the cord just below the brachial plexus in the mid-dorsal region, and just above the exit of the nerves for the lower extremities.

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<sup>1</sup>Sherrington: Observations on some Spinal Reflexes and the Interconnection of Spinal Segments. *Jour. of Phys.*, Vol. XXIX, p. 58.

<sup>2</sup>*Op. cit.*, p. 96.

<sup>3</sup>Mendelsohn: Berlin Akad. d. Wissensch., 1882, pp. 897 ff. See also *Arch. f. Anat. u. Physiol.*, 1883, *Phys. Abth.*, pp. 282 ff.

<sup>4</sup>Mendelsohn: Berlin Akad. d. Wissensch., 1883, pp. 123 ff.



In the case of hemisection and stimulation on the injured side the excitation may cross from the stimulated hind leg to its opposite and from thence to the fore extremities in weakened degree. Longitudinal median section between the brachial and lumbar plexuses only weakens the reflexes, but total transverse section in the dorsal part causes reflexes in the anterior limbs wholly to disappear. This series furnishes sufficient proof that reflex excitation is not fatally confined to any definite tract in its headward progression.

In Mendelsohn's third article<sup>1</sup> we find again, beside a confirmation of the preceding conclusions, another contradiction of Pflüger's fourth law. The excitation following a stimulus of the right fore foot spreads toward the hind limbs although with more difficulty than in the opposite direction. Sherrington, too, has shown that in a dog with hemisected cervical cord the scratch reflex can be readily produced on the side of the lesion by tickling the shoulder or neck.<sup>2</sup>

Thus at different parts of the cord the ease with which the transmission of excitation occurs, is what is to be expected from the segmental character of the spinal axis in so far as it is segmental in a functional sense. Instead of a supreme centre for the co-ordination of reflexes which was once supposed to exist in the upper parts of the spinal axis, it is now held that the cord is composed of a great number of parts more or less independent and capable of caring for a definite group of reflexes. Physiologists have been gradually led to this conception of the reflex functions of the spinal cord through the long line of researches extending from those of Lister, described in the section on Vascular Reflexes, to the work of Goltz, who tells us that the clasping reflex of the male frog is possible though the whole cord save a small portion in the brachial region be removed. Later experiments on the dog by the same experimenter<sup>3</sup> are suggestive of a similar division of function. But to Schrader, a little earlier than this, we are indebted for far-reaching experiments and for a clear-cut statement regarding the segmental character of the cord. He says:<sup>4</sup> "The series of experiments we have given teaches us that the central nervous system of the frog can be divided into a series of sections, each of which is capable of performing an independent function. It brings the central nervous system of the frog into closer relation with the central nervous system of the lower

<sup>1</sup> Mendelsohn: Berlin Akad. d. Wissensch., 1885, pp. 107 ff.

<sup>2</sup> Sherrington: *op. cit.*, p. 90.

<sup>3</sup> Goltz: Der Hund mit Verkürztem Rückenmark. *Pflüger's Arch.*, Bd. LXIII, 1896, pp. 362 ff.

<sup>4</sup> Schrader: Zur Physiol. d. Froschgehirns. *Pflüger's Arch.*, XLI, 1887, pp. 75 ff.

forms, which consists of a series of distinct ganglia that are connected by commissures. It speaks against the absolute monarchy of a single apparatus, and against the existence of different kinds of centres, and invites us to seek for the centralization in a many-sided coupling of relatively independent stations."

More striking than all other reflexes, because more accessible to the unaided eye, are the co-ordinated purposive movements of spinal animals, and their so-called spontaneous movements. The beheaded eel, *e. g.*, leaps from the heated water into which it is thrown.

Long before our period it was known that the spinal frog will wipe an acidized spot on its abdomen as if to remove the offending substance. On the other hand if the same spot be pinched by a pair of tweezers, one or both hind feet are used to push away the instrument: no attempt is made to stroke the injured surface.<sup>1</sup> This is a typical case of co-ordinated reflexes. In so far as the movement is adapted to reach an end it is purposive. The same sort of purposive co-ordination Gergens describes in the spinal dog.<sup>2</sup> When the breast or neck of such an animal is tickled the opposite hind limb is brought up to scratch the spot. Apparently, however, these movements are not always purposive. For instance a spinal dog resting upon his fore legs extended, and lying upon one hind hip—the familiar position of a resting dog—when stimulated in the way just described, often moves his hind leg in such a direction that it cannot reach the stimulated spot. Yet Gergens in an attempt to defend the purposive character of even such movements, says:<sup>3</sup> "In view of these facts I may assume that the new excitation centripetally conducted during the performance of the reflex act of movement, even without the end aimed at, to wit: the removal of the stimulus, is sufficient to weaken in a certain measure the state set up by the stimulus in the portion of the central organ in question." The same author made other experiments on the spinal frog which illustrated another case of co-ordinated purposive action. The spinal frog whose toes of one hind foot are stimulated, after a time thrusts the foot under its body as if for protection.<sup>4</sup>

Thus far we have spoken only of the co-ordinated movements of single members. The movements of locomotion even,

<sup>1</sup> Pflüger: Der sensor. Functionen d. Rückenmarks, Berlin, 1853, p. 18.

<sup>2</sup> Gergens: Ueber gekreuzte Reflexe. *Pflüger's Arch.*, Bd. XIV, pp. 340 f.

<sup>3</sup> *Op. cit.*, p. 343.

<sup>4</sup> Gergens: Einige Versuche über Reflexbewegung mit dem Einfluss-Apparat. *Pflüger's Arch.*, XIII, 1876, pp. 61 ff.

in simple spinal animals, though imperfect are yet decidedly impressive. They are of different degrees of perfection in animals of different grades. To refer to the beheaded eel again: it is evidently able to perform co-ordinated locomotor movements.<sup>1</sup> Tarchanoff found that beheaded ducks for a few hours after spinal transection perform quite elaborate movements,<sup>2</sup> They swim, dive, steer with their tails, and attempt to fly from the water. Even after they are totally beheaded their movements are no less complex and orderly. By section at different parts of the cord the author is led to decide that the co-ordinating centre for these movements is in the lumbar portion. Whether they are purely automatic or reflex is a matter he cannot decide. The spinal frog, too, Sherrington says<sup>3</sup> is capable of co-ordinated locomotion. "In the spinal frog placed in water warm enough to form a skin stimulus, *e. g.*, 36° C, I have seen co-ordinate swimming, for a short time vigorous, and executed with the normal bilateral stroke of the hind limbs. But the total co-ordination is distinctly less good than when metencephalon and myelencephalon remain. There is a tendency for the animal to dive deeper and deeper in the water: this seems due to the sunken position of the head: the loss of the semicircular canals cannot be without importance for this condition." The spinal turtle and the snake by proper stimulation move forward co-ordinately,<sup>4</sup> and Bickel confirms Sherrington and others in the declaration that the spinal frog can either leap or swim.<sup>5</sup> These phenomena occur, however, only in cases extremely successful in an operative sense. Such examples point to a vast functional complexity in the spinal cord.

Considerable attention has been given to attempts at a physiological and anatomical explanation of spinal co-ordination. Sanders-Ezn in 1867 concluded, as a result of acid stimulation of different parts of the bodily surface, that a definite movement is produced by the stimulation of every distinct point of the skin.<sup>2</sup> With equally intense stimulus an almost constantly typical form of movement is produced. Sherrington says that he has seen the point of stimulation profoundly influence the reflex reaction. "Of the four senses which pre-eminently furnish space perception, one has its end organs in the skin, an-

<sup>1</sup>See Bickel: Ueber einige Erfahrungen aus d. vergleichenden Physiol., etc., *Pflüger's Arch.*, Bd. 83, pp. 155-159.

<sup>2</sup>Tarchanoff: Ueber automatische Bewegungen bei enthaupteten Enten, *Pflüger's Arch.*, Bd. XXXIII, pp. 619-622.

<sup>3</sup>Sherrington: Schäfer's Phys., Vol. II, p. 818. See also: The spinal Animal, *Med. Chir. Trans.*, Vol. LXXXII, p. 468.

<sup>4</sup>Bickel: *op. cit.*, p. 160.

<sup>5</sup>*Op. cit.*

<sup>6</sup>See Gergens: *Pflüger's Arch.*, Bd. XIII, p. 61.

other in the musculo-articular structures, and these are therefore in great measure spinal senses. It is not surprising, then, that *per se* the locus of the stimulus is for a spinal reflex an important determinant of the resulting movement.”<sup>1</sup> But Gergens earlier<sup>2</sup> was led to believe that the locus of the stimulus is of less moment. When the toe of a spinal frog was lightly stimulated by electricity the foot was thrown out and drawn back to a different position. After stimulation at the same point a second and third time, etc., it was drawn back always to a new position and finally thrust under the body as described above.

The internal mechanism for co-ordination is yet a matter for speculation. It is more fruitful for us to inquire regarding the co-ordinating mechanisms in the large. When the bulbo-spinal frog is turned upon his back he rights himself. In explanation of such phenomena as this Steiner supposed a “righting centre.”<sup>3</sup> But as Loeb justly says:<sup>4</sup> “He does not consider the possibility that contact stimuli and the irritable structures at the periphery may be sufficient for this reaction.” Further he suggests that if we grant a “righting centre” in this case we shall be tempted to posit a “flying into the flame centre” for the moth. Thus the positing of centres can go on to infinity.

The theory proposed by Louget in 1842 in the main is still current.<sup>5</sup> “The primary condition of harmony in movements is found in the very sensation of their accomplishment. In effect how should one suppose that a man or an animal who has lost the sensation of movement executed by its members, and is not able to judge of their position, of their connection with external objects, and does not even know, so to speak, that they exist, and finally does not sense with its members the ground on which it rests, how should one suppose that such an animal is able to walk regularly, to preserve its equilibrium and to do this with energy, promptitude, and primary harmony? In this case the will has only a very incomplete effect upon the muscles: for one must not be surprised at the considerable disturbance which a profound lesion of the posterior medullary fasciæ occasions in the locomotor functions, since these fasciæ preside exclusively over sensibility.” Claude Bernard in 1858 furnished strong proof for the correctness of Louget’s theory.<sup>6</sup> Want of purposiveness in movements follows section of the sensory nerve.

<sup>1</sup> Sherrington: Schafer’s Phys., Vol. II, p. 832.

<sup>2</sup> *Op. cit.*

<sup>3</sup> Steiner: Central Nervous Systems, I, 1890, p. 39.

<sup>4</sup> Loeb: Phys. of the Brain, 1900, p. 182 (note).

<sup>5</sup> See *Pflüger’s Arch.*, Bd. XXXVII, p. 618.

<sup>6</sup> Claude Bernard: *Leçons sur la phys. et la pathologie du système nerveux*, I, 1858, pp. 246 ff.

While this view is in the main yet held as correct, it has been somewhat modified. Talma, for example, has conclusively shown that of the sensory nerves those of the muscle sense are vastly more important for co-ordination than the cutaneous nerves.<sup>1</sup> If the posterior spinal roots of a frog be severed it is able to move clumsily if at all. If only the skin, on the other hand, be removed, co-ordinate locomotion still occurs. When the posterior roots from one limb are cut and the opposite normal limb is stimulated the injured one moves, if at all, very slightly and without the character of purposiveness. Such an operation has the same effect before as after decapitation. But after section of the cord movements occur in less degree. Hence he concludes that reflex movements depend not only upon the intensity of the stimulus and not alone upon the integrity of the motor tracts. In his experiments these were left intact, and yet section of the sensory nerves effected a considerable modification of these muscular effects. The law of Longet cited above he modifies as follows:<sup>2</sup> "Because the interruption of the function of the sensory nerves very profoundly influences the movements arising in the cord, a chief condition for the harmony of movements, even for the cord, must be laid in the perception of the movement occurring. Because a cord which has lost the sensation of movements does not permit the muscles to move regularly and with their former energy, precision, and harmony, it must normally judge the position of the peripheral parts and their relation to the external world in about the same manner as the brain."

"The fact that the reflex movements, under the dominion of the cord, arising in the limbs without feeling, are much less purposive than in the normal limb, proves that the idea of the presence of a part is an important condition for the delivery through the cord of motor impulses for this part."

In Talma's work we have evidently a recurrence to the notion of a spinal cord soul which co-ordinates the movements of spinal animals. This doctrine, as we have said, was stoutly defended by Pflüger. It has occasionally arisen again since the beginning of our half century, notably in the minds of Gergens, Luchsinger, Lewes and Lange.

### VIII. THEORETICAL CONSIDERATIONS.

Pflüger ascribed the movements of spinal animals to the control of a part of a divisible soul. The purposive co-ordinated movements of reflex preparations were adduced as support for this

<sup>1</sup>Talma: Eine psy. Function d. Rückenmarks, *Pflüger's Arch.*, Bd. XXXVII, pp. 617-623.

<sup>2</sup>*Op. cit.*, p. 621 f.

view.<sup>1</sup> Lotze opposed this doctrine. The spinal animal for him was a machine, but not of the first construction. Those of a scientific turn of mind eagerly grappled with this idea because it promised to make it possible for physiologists to approximate toward exact scientific research. If Pflüger's theory were correct physiology would be difficult as a science. The influence of an independent soul changing of itself and moving things, could hardly be calculated.

Goltz demonstrated to his own satisfaction that the brainless frog does not possess a soul in the sense in which Pflüger uses the term: namely, a deliberative consciousness.<sup>2</sup> He supports the Lotzeian theory.<sup>3</sup> His experiment with the normal and the beheaded frogs in gradually heated water,<sup>4</sup> attracted wide attention because by many it was regarded as proof positive of an unconscious spinal cord. The beheaded frog rests quietly and allows itself to be cooked whereas the normal animal leaps from its danger.

Wundt, however, while admitting the value of this test, says that it does not finally prove the lack of consciousness.<sup>5</sup> No objective test can inform us of the presence or absence of consciousness in another individual. The strongest proof for the cord's unconsciousness lies in the fact that in our hours of sleeping we move our bodies without awareness at the time and the act is not subject to recall. To this the objection is raised that a dull consciousness such as the cord possesses must have a short memory. Further, says Wundt:<sup>6</sup> "If, therefore, after the loss of the brain, movements remain which have the completest similarity with voluntary movements, it does not follow that in fact these are voluntary movements. If they are instinctive activities, however, they rest just as little and as much upon pure mechanism as the voluntary movements themselves. This distinction of mechanism and pure psychic activity is, so soon as one grants that consciousness is a product of the development of the unconscious soul, no more valid." These movements are instinctive. In essentials Wundt agrees with Lotze, but takes exception to the Lotzeian declaration that an animal body whose soul has had no experiences could not perform movements after decapitation. Says Wundt:<sup>7</sup> "We may, resting upon the law of heredity,

<sup>1</sup> See also Hermann: *Archiv v. DuBois u. Reichert*, 1861, pp. 350 ff.

<sup>2</sup> Goltz: *Nervencentren d. Frosches*, 1869, p. 100. See also Königsberger *med. Jahrb.*, Bd. II, p. 189.

<sup>3</sup> Goltz: *Nervencentren*, etc., p. 82.

<sup>4</sup> Goltz: *Nervencentren*, etc., pp. 127 ff; see also Königsberger *med. Jahrb.*, Bd. II, p. 218.

<sup>5</sup> Wundt: *Menschen- u. Thierseele*, Bd. II, 1863, pp. 427 ff.

<sup>6</sup> *Loc. cit.*, p. 433.

<sup>7</sup> *Loc. cit.*, p. 434.

express the supposition that what enters ready made into the life of the single cell is a product of the development of preceding generations, so that the arousal of those purposive and unconscious movements can be derived from a practice which is not limited to the individual life." Wundt believes there are grades of consciousness, and even in acephalous animals, consciousness "has developed co-ordinately with the whole body. He says:<sup>1</sup> "The soul is separable and must be in so far as it consists in a series of separated functions."

Other support for the Lotzeian theory is furnished in the experiments by Steiner on the beheaded shark. The fish is first operated upon so that in swimming it performs circular movements. Ten hours afterward when it is beheaded it continues to swim in a circle. This, he thinks, is the after effect of the former experience.

But before going on to the more purely mechanical views we must attend to a strong reversion toward Pflüger's theory.

G. H. Lewes proceeds from the assumption that identity of tissue carries with it identity of physiological property, and that similarity in the structure and connections of organs involves corresponding similarity in function.<sup>2</sup> The histological identity of the brain and cord is more and more confirmed by microscopic investigations. In the concluding paragraph of the article cited he distinguishes between spinal soul and sensibility: "In conclusion," he says, "let it be observed that unnecessary obstacles are thrown in the way of rational interpretation when connotative terms such as spinal soul are adopted. It is one thing to assign a general physiological property, such as sensibility, to the nervous centres; another thing to assign a term which is the abstract expression of the connexus of sensibilities to any one centre. In saying that the spinal cord is *a* seat of sensation, it is not meant that it is *the* seat, nor that the sensations are specifically like the sensations of color, of sound, of taste, of smell; but they are as like these as each of these is like the other." Nowhere does Lewes define himself more clearly.

His views are more fully elaborated in the *Physical Basis of Mind*.<sup>3</sup> Objectively a sensation is a phenomenon of movement but it is separated from other phenomena by the specialty of its conditions. It is not purely mechanical. It has the character of selective adaptation which separates it from the movement of machines: that is, it combines motor impulses to suit the varying requirements of the effect to be produced. Sensibility,

<sup>1</sup> *Loc. cit.*, p. 436.

<sup>2</sup> Lewes: Sensation in the Spinal Cord, *Nature*, Vol. IX, pp. 83 f.

<sup>3</sup> Lewes: *Physical Basis of Mind*, 1877.

on the other hand, represents the property of grouping and combining stimulations.<sup>1</sup> The only ground for denying sensation to the cord rests in the assumption that the brain is the sole seat of sensation.<sup>2</sup> The lack of uniformity in reflex actions he argues is evidence of sensation. It belongs to every segment.<sup>3</sup>

But sensation has two opposite faces: the objective and the subjective. On the subjective side it is consciousness. Since we know that certain actions are consequent on certain perceptions we are justified in inferring that whenever the actions are performed, the perceptions preceded them. That the perception may have stimulated the action and yet been unaccompanied by consciousness is not evidence to the contrary. We read without consciousness of the separate letters and yet are not reading automata. So far as these actions are dependent upon vital processes they are not expressible in mechanical terms. Vital facts, especially facts of sensibility, have factors neither discernible in machines nor expressible in mechanical terms.<sup>4</sup> According to Lewes' theory, so long as neural processes continue in the separated parts of the body we may speak of a soul separable with the body.

Talma sees the reflex phenomena in the same light as Lewes. After reviewing his experiments on the co-ordination of reflexes he says:<sup>5</sup> "These experiments appear to me to furnish indisputable proof for the existence of a spinal cord soul in so far as one understands thereby a complicated action in the nerve cells, as it is generally assumed in the cells of the brain,—one which determines the kind and the mode of movements following upon sensory stimulation." Luchsinger before him had called attention to his own observation that the spinal frog will turn toward a gentle stimulus but away from a severe one and concludes:<sup>6</sup> "The desouled animal knows how to adjust itself with the greatest nicety to external circumstances." Consciousness, says Maudesley,<sup>7</sup> attends the formation of neural plexuses. It is our business to investigate the conditions not of a general consciousness but of a number of particular ones. And Marshall utters a similar view when he says:<sup>8</sup> "Only the

<sup>1</sup> *Loc. cit.*, p. 361.

<sup>2</sup> *Loc. cit.*, p. 516.

<sup>3</sup> *Loc. cit.*, p. 556.

<sup>4</sup> *Loc. cit.*, p. 361.

<sup>5</sup> Talma: Eine psychische Function d. Rückenmarks, *Pflüger's Arch.*, XXXVII, p. 621. See also the preceding section of this study.

<sup>6</sup> Luchsinger: Zur Theorie. d. Reflexe, *Pflüger's Arch.*, Bd. XXIII, 1880, pp. 308 ff.

<sup>7</sup> Maudesley: Physical Conditions of Consciousness, *Mind*, 1887, pp. 489 ff.

<sup>8</sup> H. R. Marshall: Consciousness and Biological Evolution, *Mind*, No. XXXV, 1896.



brain consciousness falls under the scope of introspective psychology, but logical considerations lead to a widening of the limits of consciousness and to the hypothesis that there is a certain mentality connected with each neural action which gives us consciousness of different grades under certain conditions of neural systematization."

Of the same school of thought is Lange who takes up the question where Pflüger left it, but tries to avoid his error: that of personification. Pflüger's experiment is more valuable and fundamental than Goltz's in which it was believed that the presence of consciousness in the spinal animal was disproven. He says:<sup>1</sup> "Let us drop personification: let us cease to seek everywhere, in the parts of the frog, thinking, feeling, acting frogs, and try instead to explain the phenomena out of simpler phenomena, *i. e.*, from reflex movements, not from the whole, the unexplained soul. Then we shall easily discover, too, that in these already so complicated sequences of sensation and movement there is afforded the beginning of an explanation of the most complicated psychological activities. This would be a path to follow up." Lange puts his faith in modes of consciousness as Lewes does. In reply to Moleschott's statement that the whole spine may be made inactive without consciousness being affected, he says:<sup>2</sup> "Good! But when it is concluded that decapitated creatures have no sensation and no consciousness, Moleschott overlooks that the head separated from the spine might show its consciousness in a way we can understand, but not the trunk. What sensation and what consciousness there may or may not be in the spinal centres when separated from the head we cannot possibly know. This only we can certainly assume: that this consciousness can do nothing that is not based in the mechanical conditions of the centripetal and centrifugal nerve conduction and the constitution of the centre."

But we must follow out further the direction set by Lotze. In one of his own later statements he emphasizes the subordinate position of mechanism:<sup>3</sup> "We cannot be surprised at the steadfastness with which the philosophy of the feelings here seeks to oppose itself as a higher view of things to the convincing representations of the mechanical view of nature. On the other hand there seems all the more necessity for an attempt to show the innocuousness of this view, which, when it forces us to sacrifice opinion that seems to be a part of our very selves, yet by what it gives back makes it possible for us to regain the satisfaction we had lost. And the more I myself have labored

<sup>1</sup> Lange: History of Materialism, 1892, Vol. III, p. 127.

<sup>2</sup> *Loc. cit.*, pp. 127-128.

<sup>3</sup> Lotze: Microcosmos, p. 46, Vol. I, 1885.

to prepare the way for the acceptance of the mechanical view of nature in the region of organic life—in which region this view seemed to advance more timidly than the nature of the thing required—the more do I now feel impelled to bring into prominence the other aspect which was equally near my heart during all those endeavors.”

His earlier representations were mediating views and were easily interpreted as favorable to either side. “But all the same it is in such mediation alone that the true source of the life of science is to be found: not, indeed, in admitting now a fragment of the one view, and now a fragment of the other, but in showing how absolutely universal is the extent and at the same time how completely subordinate the significance of the mission which mechanism has to fulfill in the structure of the world.”

Then as to the spinal soul:<sup>1</sup> “We may speak of a divisible soul, if we are thinking merely of the . . . predisposition to mental life which seems to pervade the body: but if the divided subject be supposed to be the already developed consciousness with its remembrances and experiences, and the dexterities and knowledge acquired by means of these, we could have no clear idea of what we are saying. Yet only a divisibility of the latter kind could account for the phenomena: for the capacity of acting in accordance with circumstances would be secured for the headless trunk not a whit more easily by means of an intelligence having no experience than of a purely physical mechanism as first formed. Hence there is a choice of only two views. Either we must regard the purposive character of the movements of headless cold-blooded animals as the result of an intelligence but of an intelligence not now present in the animal, but belonging to that one soul with whose seat the trunk was once in connection and from whose deliberations proceed habits of purposive actions in the central organ and continue even after all connection between it and the soul has been done away with. Or if we conclude that they must be accounted for not by echo but by the direct presence of intelligence, there is nothing to prevent us from admitting in the spinal cord a plurality of individual beings of the nature of souls, each of which might have an intelligence for itself.”

In the purposive movements of spinal animals Sherrington sees nothing psychical. A mechanical explanation is all that is necessary. He says:<sup>2</sup> “The joints and muscles of the limb

<sup>1</sup> *Loc. cit.*, p. 337.

<sup>2</sup> Sherrington: *The Spinal Animal*, *Med. Chir. Transacts.*, Vol. LXXXII, p. 466.

have been evolved contemporaneously and together in the history of the individual and the species. No muscle can therefore be thrown into action which will move the limb in any way which is an unnatural direction." And like this is Wundt's latest word:<sup>1</sup> "Adaptation can never be any other than a result of elementary practice processes. At the same time it is, however, a more complex process, since its essential character consists in a plurality of exercises which produce a definite purposeful total consequence."

When Pflüger's point of view is modified as it is by Lewes and Lange it can be neither proven nor disproven by introspection. On the other hand it seems difficult to account for complicated adaptations, either in spinal animals or in the lowest living creatures, on the assumption of a pure mechanism of either the first or the second construction. Wundt believes that in the lowest animals movements are accompanied by some degree of mentality. "In the lowest animals all movements possess not the character of reflexes . . . but the character of psychically conditioned movements."<sup>2</sup>

The soul, as Pflüger used the term in his discussion of its divisibility, is an abstraction. It is beyond the reach of empirical investigation. Lotze in his earlier discussions to which reference has been made herein, also had the notion of an abstract soul set over against a concrete mechanism. But as has just been pointed out, in a later discussion he admits a different definition: one which corresponds closely to modern definitions. He has told us that the soul is divisible in so far as it is a predisposition toward mental life. This looks toward the objective face of the question.

Reviewing the history of the fifty years with reference to progress in the theory of reflex action we see clearly that the main gain has been rather in the slow alteration of stand-points than in any sudden appearance of new facts wholly incompatible with older views. The spirit of the age—its unconscious metaphysics—has changed and along with it the metaphysics of the reflex. But a point has been reached at last at which, in the opinion of the writer, at least a partial solution of the question as between the views of Pflüger and Lotze is possible.

Putting away abstract considerations, we may define the soul objectively as that feature of the central nervous system in virtue of which the organism is enabled to profit by experience. This leaves entirely out of account any consideration of the

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<sup>1</sup> Wundt: *Phys. Psych.*, 1902, Bd. II, p. 332.

<sup>2</sup> *Loc. cit.*, p. 253.

subjective side of experience which we call consciousness. Under this definition the question of a divisible soul does not involve the question of a subjective spinal consciousness.

When soul is defined objectively as above it is open to experimental observation. The question is: Can a given organism profit by experience? In other words, can it learn? or in particular can the spinal frog learn? If it can we are justified in inferring that it has such a soul as has been described. If it has not it may fairly be regarded as a machine.